

FEEDING RESPONSES TO PREDATOR-BASED REPELLENTS IN THE MOUNTAIN BEAVER (*APLODONTIA RUFA*)¹

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Abstract. Predator odors have potential as feeding repellents for mammalian herbivores, including *Aplodontia rufa*, the mountain beaver. However, the repellency of major chemical constituents of natural predator scents for this species has not been evaluated. In this study, the effects of several synthetic sulfur compounds from predator scents on feeding by mountain beavers were assessed and compared to the effects of coyote (*Canis latrans*) urine. Retrieval of food by mountain beavers from bowls scented with either coyote urine, diluted with water to different concentrations, synthetic components of predator scents, or control odorants was studied. The following synthetic compounds were tested: Δ^1 -Isopentenyl methyl sulfide (IMS), a compound present in urine from several canid species; 2,2 dimethylthietane (DMT), a major constituent in anal gland secretion from the mink (*Mustela vison*); a 1:1 mixture of 2-propylthietane (PT) and 3-propyl-1,2-dithiolane (PDT), compounds occurring in anal gland secretions from the stoat (*Mustela erminea*) and the ferret (*Mustela putorius*). Habituation to PT plus PDT was studied by measuring consumption of dry pellets during continuous exposure to these compounds for 5 d. In two-choice feeding trials mountain beavers retrieved significantly more food from bowls scented with water than from bowls scented with coyote urine. Dilution of urine had no statistically significant effect on food retrieval, but repellency tended to decrease with decreasing concentration. Mountain beavers retrieved less food scented with a 1:1 mixture of PT and PDT, compared to controls. However, they rapidly habituated to this mixture. None of the other compounds caused an avoidance response. These results show that complex natural predator scents are more effective feeding repellents than some of their major volatile components alone.

Key words: *Aplodontia rufa*; feeding repellents; mountain beaver; predator odors.

INTRODUCTION

Damage by mountain beaver severely limits regeneration of conifer forests in the Pacific Northwest. This primitive, herbivorous rodent causes millions of dollars

of losses each year by harvesting plant material for food and storage in underground burrows (Feldhamer and Rochelle, 1982, Campbell, 1994). Currently, trapping, poisoning, and mechanical barriers are the most frequently used control methods. Habitat manipulation and destruction of burrow systems are also practiced. Each of these methods is costly and with the exception

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tested: 10 and 1 mg/mL. The concentration of 10 μ g/mL approximated the concentration of the compound in our pool of coyote urine as determined by HPLC analysis. Light mineral oil served as control in both series of trials.

Stimulus fluids (500 μ L) were presented in plastic mesh capsules (HistoPrep, Fisher Scientific, USA, 25 \times 6 mm) lined with filter paper. These scent dispensers were placed into each bowl, leaving the food untainted. They allowed animals to smell the stimuli but prevented contact with odorants. All subjects were tested with the lower concentration first, followed by the higher concentration. Choice tests offered 20 g of apple per bowl for 2 h.

Experiment 3

The repellency of DMT was tested. Informal screening of DMT, using a few animals not included in the experiment, had suggested that the compound is not aversive. Therefore, in the present experiment whole coyote urine was tested on the same subjects in a counter-balanced design, in order to ascertain that possible failure to respond to DMT was not due to general habituation to predator scents.

DMT was prepared for testing by dissolving 100 μ L in 2 g of petroleum jelly. This preparation reduces feeding in European wild rabbits, woodmice, and voles (Robinson 1990). For each trial, 30 mg of DMT jelly was placed into a paper-lined HistoPrep capsule. Petroleum jelly (30 mg) served as a control odorant. Paper-lined HistoPrep capsules also served as dispensers for 500 μ L of coyote urine and 500 μ L of water.

Half of all subjects tested on each day received choices between DMT and petroleum jelly; the other half received choices between coyote urine and water. Tests lasted for 1 h, with 15 g of diced apple offered in each food bowl.

Experiment 4

The effect of commercial slow-release devices containing synthetic mustelid scent, i.e., a 1:1 mixture of PT and PDT, was tested. Blank plastic rods of the same dimensions as the devices served as controls. Scented devices and controls were enclosed in unlined HistoPrep capsules that were placed into bowls containing 20 g of diced apple. Tests lasted 2 h.

Bioassay tests, experiment 5

The effects of long-term exposure to PT-PDT devices on food consumption was investigated using five subjects. In the course of this habituation experiment, each animal was exposed to PT and PDT continuously for 5 d while housed in a large room (3.5 \times 3.5 m). The room contained the subject's nest box, two metal tunnels (120 cm long, 15 cm diameter) to increase environmental complexity, a water bowl, and two feeding stations located 3 m from each other. One feeding station was scented using a PT-PD device enclosed in a

HistoPrep capsule, the other station contained a capsule with a blank device.

Feeding stations consisted of translucent plastic boxes (40 \times 28 cm, \times 23 cm high) with 13 \times 13 cm entrances. These boxes were used to concentrate volatiles emanating from the HistoPrep capsule taped to the back wall of each box. One of the two feeding stations, including the bowl, always was used to present predator scent, while the other always was used to present control scent.

Each subject was introduced into the room 24 h before predator scent was presented. During this period, 70 g of dry pellets were available in each feeding station, containing empty HistoPrep capsules. Dry chow was the only food available throughout the adaptation and test periods.

A 5-d test period followed adaptation. Each day at 1000 chow remaining in the feeding stations was removed and weighed, 70 g of fresh chow were placed in each feeding station, and HistoPrep capsules were supplied with fresh devices. The location of boxes in the room remained constant throughout the 5 d of testing, but positions of predator- and control-scented stations were determined daily at random. Methods used in Experiment 5 are identical to those employed in a previous study on habituation to coyote urine (Epple et al. 1993), with the exception that HistoPrep capsules rather than pieces of perforated tubing were used as scent dispensers.

RESULTS

Experiment 1

A three-factor ANOVA in which sex of subject was treated as an independent factor and differently scented stimulus bowls and concentrations were treated as dependent factors showed that there was a significant difference in retrieving of urine-scented as compared to water-scented food ($F = 8.53$, $P < 0.05$) but no difference among stimulus concentrations. In addition, the interaction among the factors for stimulus type, concentration, and sex of subject was significant ($F = 3.01$, $P < 0.05$). Otherwise, there were no significant differences (Fig. 1).

Post hoc *t* tests showed that subjects, as a group, retrieved significantly more food from water-scented bowls than from bowls scented with 100% urine ($F = 12.23$, $P < 0.005$) or with 50% urine ($F = 7.07$, $P < 0.05$). Males, as a subgroup, exhibited a significant preference for water-scented food over food scented with 100% urine only ($F = 23.78$, $P < 0.01$). Females, as a subgroup, took significantly more food from bowls scented with water than from bowls scented with 50% urine only ($F = 7.43$, $P < 0.05$). However, females but not males showed a strong trend to prefer water-scented food in response to all urine concentrations (Fig. 1).

Experiment 2

A three-factor ANOVA in which sex of subject was treated as an independent factor and stimulus bowls

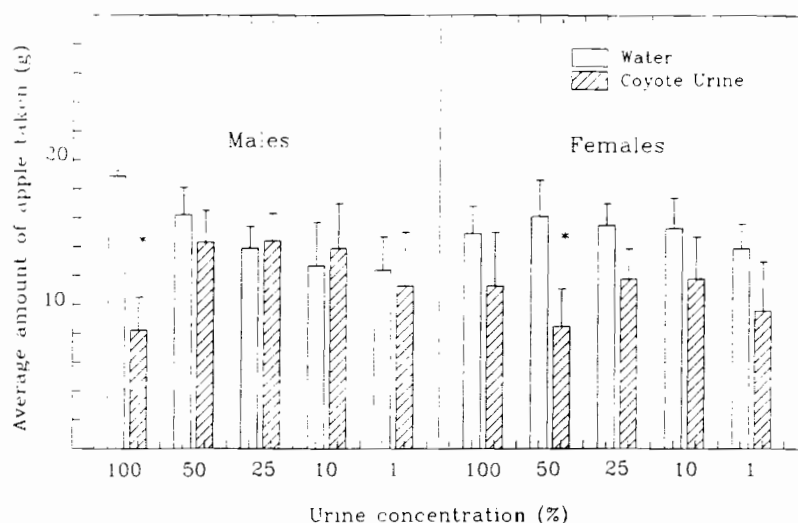


FIG. 1. Average amount of apple retrieved by male and female mountain beavers from bowls scented with different concentrations of coyote urine and from bowls scented with water; *significant difference. Data are means and 1 SE.

and IMS concentrations were treated as dependent factors failed to reveal any significant differences (Fig. 2). IMS did not affect food retrieval.

Experiment 3

A three-factor ANOVA in which sex of subject was treated as an independent factor and stimulus bowls and stimulus types as dependent factors showed that there were significant differences between males and females ($F = 30.6, P < 0.001$), between stimulus bowls ($F = 22.3, P < 0.001$), and an interaction between bowls and stimulus types ($F = 9.44, P < 0.05$). The analysis was interpreted in terms of two-way interactions. Post hoc *t* tests indicated that coyote urine significantly reduced food retrieval compared to water in male and female subjects ($F = 8.66, P < 0.05$), but that DMT had no effect (Fig. 3). Females retrieved

significantly less apple from coyote urine-scented bowls than did males ($F = 14.5, P < 0.005$), but there were no sex differences in food caching in response to DMT.

Experiment 4

A two-factor ANOVA in which sex was treated as an independent factor and stimulus type as a dependent factor, showed that the animals, as a group, retrieved less apple from bowls scented with PT-PDT devices ($F = 8.1, P < 0.05$). There was no significant difference between male and female subjects and no interaction between sex and stimulus type (Fig. 4).

Experiment 5

A three-factor ANOVA, in which sex was treated as an independent factor, and days of exposure and stim-

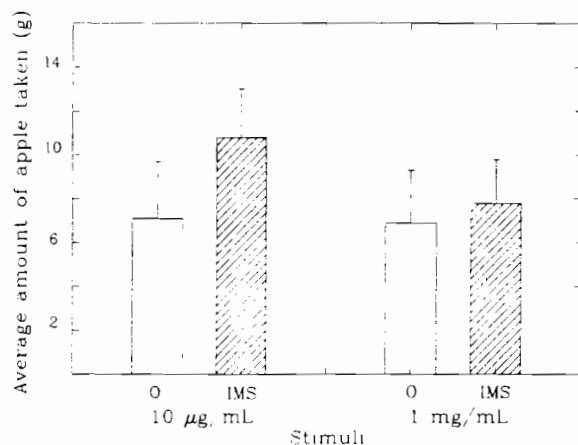


FIG. 2. Average amount of apple retrieved from bowls scented with two concentrations of IMS and from bowls scented with mineral oil (O). Results from male and female mountain beavers are combined. Data are means and 1 SE.

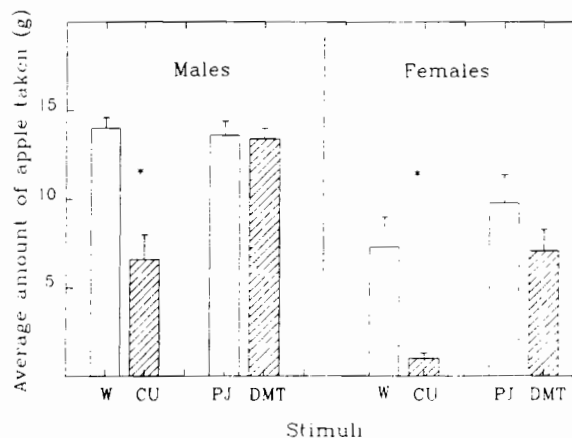


FIG. 3. Average amount of apple retrieved by male and female mountain beavers when offered choices between coyote urine (CU) and water (W) scented food, or between DMT and petroleum jelly (PJ) scented food; *significant difference. Data are means and 1 SE.

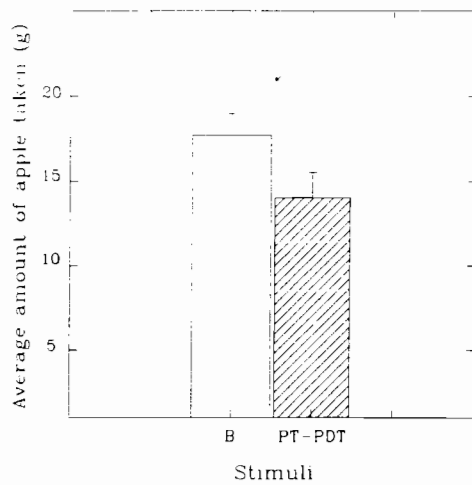


FIG. 4. Average amount of apple retrieved from bowls scented with PT-PDT devices and from bowls scented with blank devices (B). Results from male and female mountain beavers are combined, *significant difference. Data are means and 1 SE.

ulus bowls were treated as dependent factors, failed to reveal significant differences (Fig. 5). This indicates that the PT-PDT devices did not influence feeding when subjects were continuously exposed to them.

DISCUSSION

The present results are consistent with our previous finding (Epple et al. 1993, Nolte et al. 1993, 1994) that coyote urine is an effective feeding deterrent for the mountain beaver. However, feeding from urine-scented sources is not completely suppressed, and there is individual variability in response to this stimulus. The interaction among sex of subject, stimulus type, and stimulus dilution found in Experiment 1 and the significant sex difference in response to whole coyote urine in Experiment 3 suggest that males are less sensitive than females to aversive urinary cues. Mountain

beaver males are considerably heavier than females (Nowak 1991). Their absolute energy requirements are probably higher than those of females, and this may cause them to take a higher predation risk during foraging.

The sulfide from canid urine (IMS) and the major sulfur constituent of mink anal sac fluid (DMT) had no effect on food retrieval. PT and PDT reduced food retrieval for short periods of time. Subjects habituated quickly to these odors, however. This is in strong contrast to the mountain beavers' responses to coyote urine. When five animals were tested with whole coyote urine under conditions identical to those used in Experiment 5, no habituation occurred during the entire 5-d test period (Epple et al. 1993). In another study, plants sprayed with coyote urine were avoided for up to 3 wk (Nolte et al. 1993).

IMS and DMT are not aversive to mountain beavers, in spite of the fact that they are major volatile constituents of natural predator scents that are effective repellents for this species. This indifference is surprising, in light of the widespread repellency of sulfur-containing compounds and our previous finding that precipitation of such compounds in coyote urine reduces its repellent qualities for mountain beavers (Nolte et al. 1994). Moreover, several other species respond to DMT and IMS. DMT is a strong feeding deterrent for snowshoe hares (Sullivan and Crump 1984) and European wild rabbits and reduces trap entry in wood mice and bank voles (Robinson 1990). IMS also reduces browsing in snowshoe hares (Sullivan and Crump 1986a). PT and PDT, to which mountain beavers habituate quickly, are strong, long-lasting repellents for a number of small mammals (Sullivan and Crump 1984, Sullivan et al. 1988a, b, 1990a, b, Merckens et al. 1991).

Mountain beavers respond to the same natural predator scents that repel other herbivores but are largely indifferent to some of the constituents to which other

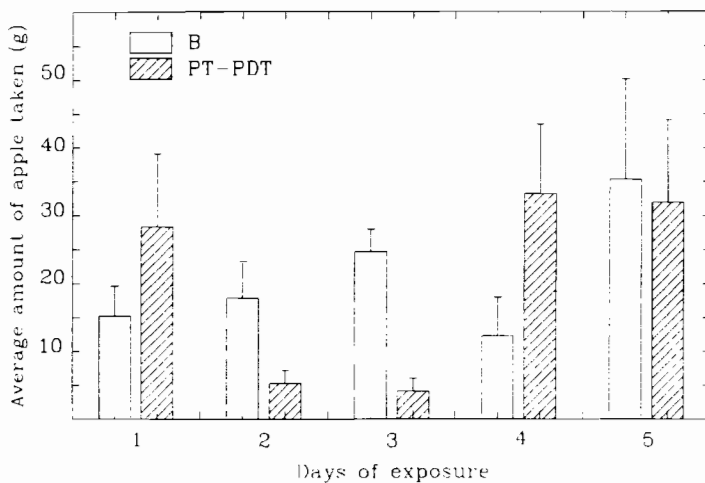


FIG. 5. Average amount of dry chow taken from feeding stations scented with PT-PDT devices and from feeding stations scented with blank devices (B) during 5 d of exposure to the devices. Results from male and female mountain beavers are combined. Data are means and 1 SE.

species respond strongly. This could be interpreted in several ways. The aversiveness of natural predator scents for mountain beavers may depend on one or a few key compounds other than those tested here. Conversely, mountain beavers may respond to a mixture of compounds present in natural predator scents. Although the synthetic compounds tested in the present study may be active components of such scent mixtures, they may not have a measurable repellency by themselves. Some other herbivores also respond more strongly to complex natural scents than to single compounds or simple mixtures (Vernet-Maury et al. 1984, Sullivan and Crump 1986a, Abbott et al. 1990).

Although many herbivores are repelled by selected key compounds in predator scents, these compounds may not be identical for each species that responds to the natural scent mix. Moreover, additional constituents of the mixture may enhance the effectiveness of key compounds in a species-specific manner. Thus, predator-derived compounds have high potential as feeding repellents for a number of herbivores, including mountain beavers. However, the constituents of natural predator scents to which this species is most responsive must be isolated and identified before effective repellents can be formulated.

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LITERATURE CITED

- Abbott, D. H., D. A. Baines, C. G. Faulkes, D. C. Jennens, P. C. Y. K. Ning, and A. J. Tomlinson. 1990. A natural deer repellent: chemistry, and behavior. Pages 599-609 in D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, editors. Chemical signals in vertebrates V. Oxford University Press, Oxford, UK.
- Albone, E. S. 1984. Mammalian semiochemistry. John Wiley and Sons, New York, New York, USA.
- Andelt, W. F., D. L. Baker, and K. P. Burnham. 1992. Relative preference of captive cow elk for repellent treated diets. *Journal of Wildlife Management* 56:164-173.
- Andersen, K. K., and D. T. Bernstein. 1980. Sulfur compounds in mustelids. Pages 399-406 in D. Cavallini, G. E. Gauli, and V. Zappia, editors. Natural sulfur compounds. Plenum, New York, New York, USA.
- Arnould, C., and J. P. Signoret. 1993. Sheep food repellents: efficacy of various products, habituation, and social facilitation. *Journal of Chemical Ecology* 19:225-236.
- Bailey, S., P. J. Bunyan, and J. M. J. Page. 1980. Variation in the levels of some components of the volatile fraction of urine from captive red foxes and its relationship to the state of the animal. Pages 391-403 in D. Müller-Schwarze and R. M. Silverstein, editors. Chemical signals in vertebrates and aquatic invertebrates. Plenum, New York, New York, USA.
- Boag, B., and J. A. Mlotkiewicz. 1991. Evaluation of an odour derived from lion faeces on the behavior of wild rabbits. *Tests of Agrochemicals and Cultivars* 12:18-19.
- Brinck, C., S. Erlinge, and M. Sandell. 1983. Anal sac secretions in mustelids: a comparison. *Journal of Chemical Ecology* 9:727-745.
- Buglass, A. J., F. M. C. Darling, and J. S. Waterhouse. 1990. Analysis of the anal sac secretion of the Hyaenidae. Pages 65-69 in D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, editors. Chemical signals in vertebrates V. Oxford University Press, Oxford, UK.
- Campbell, D. L. 1994. Mountain beaver. Pages B53-B60 in S. E. Hyngstrom and R. M. Timm, editors. Prevention and control of wildlife damage. Volume 2. University of Nebraska Cooperative Extension Service, in cooperation with United States Department of Agriculture, Animal and Plant Health Inspection Service, Animal Damage Control, and Great Plains Agricultural Council, Lincoln, Nebraska, USA.
- Crump, D. R. 1980a. Anal gland secretion of the ferret (*Mustela putorius forma furo*). *Journal of Chemical Ecology* 6:837-844.
- . 1980b. Thietanes and dithiolanes from the anal gland of the stoat (*Mustela erminea*). *Journal of Chemical Ecology* 6:341-347.
- Epplé, G., J. R. Mason, D. L. Nolte, and D. L. Campbell. 1993. Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). *Journal of Mammalogy* 74:715-722.
- Feldhamer, G. A., and J. A. Rochelle. 1982. Mountain beaver—*Aplodontia rufa*. Pages 167-175 in J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Gorman, M. L. 1984. The responses of prey to stoat (*Mustela erminea*) scent. *Journal of Zoology (London)* 202:419-423.
- Jorgenson, J. W., M. Novotny, M. Carmack, G. B. Copland, S. R. Wilson, S. Katona, and W. K. Whitten. 1978. Chemical scent constituents in the urine of the red fox (*Vulpes vulpes* L.) during the winter season. *Science* 199:796-798.
- Lewinson, R., J. N. Bean, E. V. Aronov, and J. R. Mason. 1994. Similarities between Big Game Repellent and predator urine repellency to white-tailed deer: the importance of sulfur and fatty acids. Eastern Wildlife Damage Management Conference 6, in press.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Macdonald, D. W. 1985. The carnivores: Order Carnivora. Pages 619-722 in R. E. Brown and D. W. Macdonald, editors. Social odours in mammals. Volume 2. Clarendon, Oxford, UK.
- Mason, J. R., G. Epplé, and D. L. Nolte. 1994. Semiochemicals and improvements in rodent control. Pages 327-346 in B. E. Galef, M. Mainardi, and P. Valsecchi, editors. Behavioral aspects of feeding: basic and applied research in mammals. Harwood Academic, Chur, Switzerland.
- Mattina, M. J. I., J. J. Pignatello, and R. K. Swihart. 1991. Identification of volatile components of bobcat (*Lynx rufus*) urine. *Journal of Chemical Ecology* 17:451-462.
- Mayer, A. 1974. Eine einfache Synthese von 2,2-Dimethylthietan. *Helvetica Chimica Acta* 57:2514.
- Merkens, M., A. S. Harestad, and T. Sullivan. 1991. Cover and efficacy of predator-based repellents for Townsend's vole, *Microtus townsendii*. *Journal of Chemical Ecology* 17:401-412.
- Müller-Schwarze, D. 1972. Responses of young black-tailed deer to predator odors. *Journal of Mammalogy* 53:393-394.
- Murphy, E. L., R. A. Flath, D. R. Black, T. R. Mon, R. Teranishi, R. M. Tim, and W. E. Howard. 1978. Isolation, identification and biological activity assay of chemical fractions from estrus urine attractive to the coyote. Pages 66-77 in R. W. Bullard, editor. Flavor chemistry of animal foods. American Chemical Society Symposium Series

- Number 67. American Chemical Society, Washington, D.C., USA.
- Nolte, D. L., J. P. Farley, D. L. Campbell, J. R. Mason, and G. Epple. 1993. Potential repellents to prevent mountain beaver damage. *Crop Protection* **12**:624–626.
- Nolte, D. L., J. R. Mason, G. Epple, E. Aronov, and D. L. Campbell. 1994. Why are predator urines aversive to prey? *Journal of Chemical Ecology* **20**:1505–1516.
- Nowak, R. M. 1991. *Walker's mammals of the world*. Fifth edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Raymer, J., D. Wiesler, M. Novotny, C. Asa, U. S. Seal, and L. D. Mech. 1984. Chemical scent constituents in urine of wolf and their dependence on reproductive hormones. *Journal of Chemical Ecology* **12**:297–314.
- Robinson, I. 1990. The effect of mink odor on rabbits and small mammals. Pages 567–572 in D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, editors. *Chemical signals in vertebrates V*. Oxford University Press, Oxford, UK.
- Schildknecht, H., C. Birkner, and D. Krauss. 1981. Struktur und Wirkung der Musteliden-Ökonomie II. Erweiterte Analyse des Analbeutelsekretes des Nerzes *Mustela vison* L. *Chemiker Zeitung* **105**:273–286.
- Schultz, T. H., S. M. Kruse, and R. A. Flath. 1985. Some volatile constituents of female dog urine. *Journal of Chemical Ecology* **11**:169–175.
- Schultz, T. H., R. A. Flath, D. J. Stern, T. R. Mon, R. Teranishi, S. McKenna Kruse, B. Butler, and W. E. Howard. 1988. Coyote estrous urine volatiles. *Journal of Chemical Ecology* **14**:701–712.
- Sokolov, V. E., V. E. Albone, P. F. Flood, P. F. Heap, M. Z. Kagan, V. S. Vasilieva, V. V. Roznov, and E. P. Zinkevich. 1980. Secretion and secretory tissues of the anal sac of the mink, *Mustela vison*. *Journal of Chemical Ecology* **6**:805–825.
- Sullivan, T. P., and D. R. Crump. 1984. Influence of mustelid scent gland compounds on the suppression of feeding by snowshoe hares (*Lepus americanus*). *Journal of Chemical Ecology* **10**:1809–1821.
- Sullivan, T. P., and D. R. Crump. 1986a. Feeding responses of snowshoe hares (*Lepus americanus*) to volatile constituents of red fox (*Vulpes vulpes*) urine. *Journal of Chemical Ecology* **12**:229–239.
- Sullivan, T. P., and D. R. Crump. 1986b. Avoidance response of pocket gophers (*Thomomys talpoides*) to mustelid anal gland compounds. Pages 519–531 in D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, editors. *Chemical signals in vertebrates IV, ecology, evolution, and comparative biology*. Plenum, New York, New York, USA.
- Sullivan, T. P., D. R. Crump, and D. S. Sullivan. 1988a. Use of predator odors as repellents to reduce feeding damage by herbivores. III. Montane and meadow voles (*Microtus montanus* and *Microtus pennsylvanicus*). *Journal of Chemical Ecology* **14**:363–377.
- Sullivan, T. P., D. R. Crump, and D. S. Sullivan. 1988b. Use of predator odors as repellents to reduce feeding damage by herbivores. IV. Northern pocket gophers (*Thomomys talpoides*). *Journal of Chemical Ecology* **14**:379–389.
- Sullivan, T. P., D. R. Crump, H. Wieser, and A. Dixon. 1990a. Comparison of release devices for stoat (*Mustela erminea*) semiochemicals used as montane vole (*Microtus montanus*) repellents. *Journal of Chemical Ecology* **16**:951–957.
- Sullivan, T. P., D. R. Crump, H. Wieser, and A. Dixon. 1990b. Responses of pocket gophers (*Thomomys talpoides*) to an operational application of synthetic semiochemicals of stoat (*Mustela erminea*). *Journal of Chemical Ecology* **16**:941–949.
- Sullivan, T. P., L. O. Nordstrom, and D. S. Sullivan. 1985a. Use of predator odors as repellents to reduce feeding damage by herbivores. I. Snowshoe hares (*Lepus americanus*). *Journal of Chemical Ecology* **11**:903–909.
- Sullivan, T. P., L. O. Nordstrom, and D. S. Sullivan. 1985b. Use of predator odors as repellents to reduce feeding damage by herbivores. II. Black-tailed deer (*Odocoileus hemionus columbianus*). *Journal of Chemical Ecology* **11**:921–935.
- Swihart, R. K. 1991. Modifying scent marking behavior to reduce woodchuck damage to fruit trees. *Ecological Applications* **1**:98–103.
- Vernet-Maury, E. 1980. Trimethyl-thiazoline in fox feces: a natural alarming substance for the rat. Page 407 in H. van der Starre, editor. *Olfaction and taste VII*. Information Retrieval, Washington, D.C., USA.
- Vernet-Maury, E., B. Constant, and J. Chanel. 1992. Repellent effect of trimethyl-thiazoline in the wild rat *Rattus norvegicus* Berkenhout. Pages 305–310 in R. L. Doty and D. Müller-Schwarze, editors. *Chemical signals in vertebrates VI*. Plenum, New York, New York, USA.
- Vernet-Maury, E., E. H. Polak, and A. Demael. 1984. Structure/activity relationship of stress inducing odorants in the rat. *Journal of Chemical Ecology* **10**:1007–1018.
- Wheeler, J. W., D. W. Von Endt, and C. Wammer. 1975. Thiomethyl-pentane-2,3-dione. A unique natural compound from the striped hyaena. *Journal of the American Chemical Society* **97**:441.
- Wilson, S. R., M. Carmack, M. Novotny, J. W. Jorgenson, and W. K. Whitten. 1978. Δ^3 -Isopentenyl methyl sulfide. A new terpenoid in the scent mark of the red fox. *Journal of Organic Chemistry* **43**:4675–4676.